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A new species of *Iconella* (Mason, 1981) (Hymenoptera, Braconidae, Microgastrinae), a parasitoid of *Melitara subumbrella* (Dyar, 1925) cactus moth larvae from New Mexico with biological notes and an updated key to the American *Iconella* species

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Abstract

We describe the wasp *Iconella melitaraevora* **sp. nov.** (Braconidae, Microgastrinae), a parasitoid of *Melitara subumbrella* caterpillars (Lepidoptera, Pyralidae, Phycitinae). Multiple wasp cohorts were reared from hosts collected in a montane dryland habitat of New Mexico, USA. This is the first case of gregariousness in *Iconella*. An updated key to American *Iconella* species is provided. We present a maximum likelihood tree using the cytochrome c oxidase subunit I (COI) locus of this species relative to other described *Iconella* species from the Americas. We also describe the biology and environmental conditions where *Iconella melitaraevora* **sp. nov.** was discovered in the context of its prickly pear cactus (*Opuntia* Mill.) herbivore host. The potential biological control capacity of microgastrine wasps which attack prickly pear specialist herbivores is discussed.

Keywords

CO1, gregarious, maximum likelihood tree, Nearctic, *Opuntia*, Phycitinae, species description, wasp

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Introduction

Microgastinae is a lineage of parasitoids wasps (Hymenoptera: Braconidae) that attack Lepidoptera with approximately 3,000 named species worldwide and is estimated to comprise 30,000 to 50,000 species when undescribed species are included (Rodriguez et al. 2013; Fernandez-Triana et al. 2020). *Iconella* (Mason, 1981), is a small genus within Microgastrinae with four previously described species from North America, the Caribbean, and South America (Fernandez-Triana et al. 2013). *Iconella* are known to be solitary, koinobiont, endoparasitoids of shelter-forming microlepidopteran larvae (Whitfield et al. 1997; Fernandez-Triana et al. 2013). Besides this fundamental natural history, the ecology of *Iconella* species is not well understood aside from the Neotropical species *I. isolata* (Muesebeck, 1955) which has been investigated as a biological control agent of crop pests (Bennett 1960; Bartlett 1978).

Until now, two species were known from North America, *I. canadensis* Fernández-Triana 2013 and *I. etiellae* (Viereck 1911). Here, we describe a new species from high-elevation, dryland habitat in the southern Rocky Mountains, *Iconella melitaraevora* sp. nov. We present information on its biology and compare it with other species in the genus. We conclude this contribution with a discussion of biological control implications of microgastrine wasps that attack *Opuntia* specialist Lepidoptera.

Methods

Opuntia phaeacantha Engelm. (caterpillar host plant) pads and parasitized *Melitara subumbrella* (Dyar 1925) caterpillars which fed upon *O. phaeacantha* were collected on 23 August 2023 in Santa Fe County, New Mexico on the property of Hillary and David Armstrong (35.2216, -106.2080). The collections were made at 2225 m a.s.l. in piñon-juniper woodland near the transition from piñon-juniper to Rocky Mountain conifer forest ecoregion. The vegetation of this semi-arid ecosystem is characterized by piñon pine (*Pinus edulis* Engelm., Pinaceae), one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg., Cupressaceae), desert prickly pear (*Opuntia phaeacantha*, Cactaceae), tree cholla (*Cylindropuntia imbricata* (Haw.) F.M.Knuth, Cactaceae), and Gambel oak (*Quercus gambelii* Nutt., Fagaceae). Temperature range varies dramatically in this region, both daily and seasonally. The average annual maximum temperature is 17 °C, with high temperatures exceeding 38 °C occasionally, and extended periods below -18 °C from November to March. The average yearly minimum temperature is 4 °C. Precipitation is driven by monsoons from June to August, with the area receiving an average of 50 cm rainfall annually. The area receives 152 cm of snow on average from November to March.

The *M. subumbrella* larvae were brought to The University of Texas at Austin, Brackenridge Field Laboratory on 03 September 2023 within pads of their host plant. The pads were maintained in containment at room temperature, with indirect sunlight. Pads with actively feeding *M. subumbrella* larvae were placed inside large plastic

boxes on top of 5 cm of ProMix BX mycorrhizae growth media (Québec, Canada) within white mesh, emergence cages. Emergent wasps were collected with an aspirator and preserved in 100% ethanol between 27 November and 25 December 2023.

Wasp and caterpillar DNA extractions were performed at the Brackenridge Field Laboratory using the DNeasy Blood & Tissue Kit (Qiagen, Germany). A region of approximately 450–750 bp of the mitochondrial gene CO1 was amplified with degenerate primer sets LCO1490-F/HCO2198-R (Vrijenhoek 1994), followed by Sanger sequence analysis at Eton Bioscience Inc (California USA). *Melitara subumbrella* was identified as the caterpillar host following description and ecological context provided by Mann (1969) as well as via BLAST search query of the CO1 region on GenBank (Process ID NACMA004-25). CO1 sequences of other Nearctic and Neotropical *Iconella* species were downloaded from GenBank and the Barcode of Life Data System (BOLD; (Ratnasingham and Hebert 2007) (Table 1). *Iconella* CO1 sequences were aligned using MUSCLE version 5 (Edgar 2004) with default parameters in Geneious version 8 (Kearse et al. 2012). Maximum likelihood trees were constructed in MEGA 11 with a Tamura-Nei substitution rate model (Tamura et al. 2021) and 10,000 bootstrap replicates to infer generic placement. *Iconella melitaraevora* CO1 sequences were accessioned on BOLD (Process ID NACMA001-24).

Morphological terms follow Huber and Sharkey (1993), Whitfield et al. (1997), and Fernandez-Triana et al. (2014), which are included in the Hymenoptera Anatomy and Ontology (HAO) website (http://portal.hymao.org/projects/32/public/ontology/). The abbreviations F2 and F14 are used for antennal flagellomeres 2 and 14; T1 and T2 are used for metasomal mediotergites 1 and 2; and L and W refer to length and width. A diagnostic description is provided, followed by some measurements of morphological traits commonly used in Microgastrinae (Fernandez-Triana et al. 2014). The holotype and most paratype specimens are deposited in The University of Texas at Austin Insect Collection in Austin, TX (UTIC), with male and female paratypes also deposited in the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, Canada (CNC) and the Smithsonian Institute in Washington D.C., USA (USNM).

Table 1. Biological metadata, NBCI GenBank and BOLD accession numbers for specimens with COI sequences analyzed in Fig. 2.

Species	Collection locality	NCBI accession	BOLD processID	Hosts
Apanteles opuntiarum	Santa Fe, Argentina		NACMA002-24	*Cactoblastis cactorum* (Pyralidae)
Iconella melitaraevora	New Mexico, U.S.A.		NACMA001-24	*Melitara subumbrella* (Pyralidae)
Iconella etiellae	California, U.S.A.	JQ851291.1	HYCNE1332-11	*Etiella zinckenella* (Pyralidae)
				Melitara junctolineella (Pyralidae)
				Psorosina hammondi (Pyralidae)
				Ufa rubedinella (Pyralidae)
Iconella canadensis	Ontario, Canada		HYCNE1310-11	*Epinotia solandriana* (Tortricidae)
				Acrobasis betulella (Pyralidae)
Iconella andydeansi	Alajuela, Costa Rica	KC685304.1	ACGBA2903-12	undescribed species phyjanzen021 "Janzen855" (Pyralidae)
Iconella jayjayrodriguezae	Alajuela, Costa Rica	JQ851067.1	ASHYE1188-09	undescribed species "spiloBioLep01 BioLep414" (Crambidae)

Data resources

Videos and images of the interaction are provided in Suppl. material 1 available on GitHub via Zenodo at https://doi.org/10.5281/zenodo.14589691 (Morrison et al. 2024).

Results

***Iconella melitaraevora* Fernandez-Triana, sp. nov.**
https://zoobank.org/FFB666D4-3A86-4E19-8ABA-5D1A4B589EB8

Holotype. United States • ♀ (UTIC) • New Mexico, Santa Fe, Armstrong residence; 35.2268, -106.2080; 17.xi.2023; ex. *Melitara subumbrella* (Lepidoptera, Pyralidae, Phycitinae); Wyatt Armstrong & Colin Morrison colls; UTIC396104.

Paratypes. Same locality and dates as holotype. UTIC: ♀ UTIC396102, ♂ UTIC396103, ♀ UTIC396105; CNC: ♂ ISRL148316.04; USNM: ♂ ISRL148316.06, ♀ ISRL148312.05.

Distribution. New Mexico, USA. These specimens are the only known representatives of this species.

Etymolgy. Named after its lepidopteran host species.

Diagnostic description also see key below. This species can be recognized as *Iconella* based on the features first described by Mason (1981) and further expanded and discussed in Fernandez-Triana et al. (2013, 2020), namely: a sinuated vein cu-a in the hind wing and the presence of a median longitudinal carina on the propodeum. *Iconella melitaraevora* is very distinctive from most other described species in the New World (Fig. 1). *Iconella isolata*, a species recorded from the Caribbean and South America, has much lighter coloration of hind legs and veins in forewing, as well as mostly transparent or whitish pterostigma, with only thin brown margins (pterostigma almost completely brown, with only small whitish spot anteriorly in *melitaraevora*). Two species recorded from Central America (Costa Rica and Mexico), *I. andydeansi* and *I. jayjayrodriguezae* both have mostly transparent or whitish pterostigma, with only thin brown margins (pterostigma almost completely brown, with only small whitish spot anteriorly in *melitaraevora*); T1 width at anterior margin 3.1× or more its width at posterior margin (T1 width at anterior margin 2.4–2.6× its width at posterior margin in *melitaraevora*); metatibia with smaller darker area posteriorly and with larger yellow spot on anterior half of first segment of metatarsus (metatibia dark on posterior half and first segment of metatarsus with very small yellow spot anteriorly in *melitaraevora*). *Iconella canadensis*, recorded from Eastern Canada, has different pterostigma color (mostly transparent or whitish versus mostly brown in *melitaraevora*); comparatively smaller ocelli size (ocular-ocellar line 1.6× posterior ocellus diameter versus 2.0× *melitaraevora*); and shorter ovipositor sheath (ovipositor sheath length 0.8× or less metatibial length versus 1.06–1.12× in *melitaraevora*). Also see key below for additional diagnostic description.

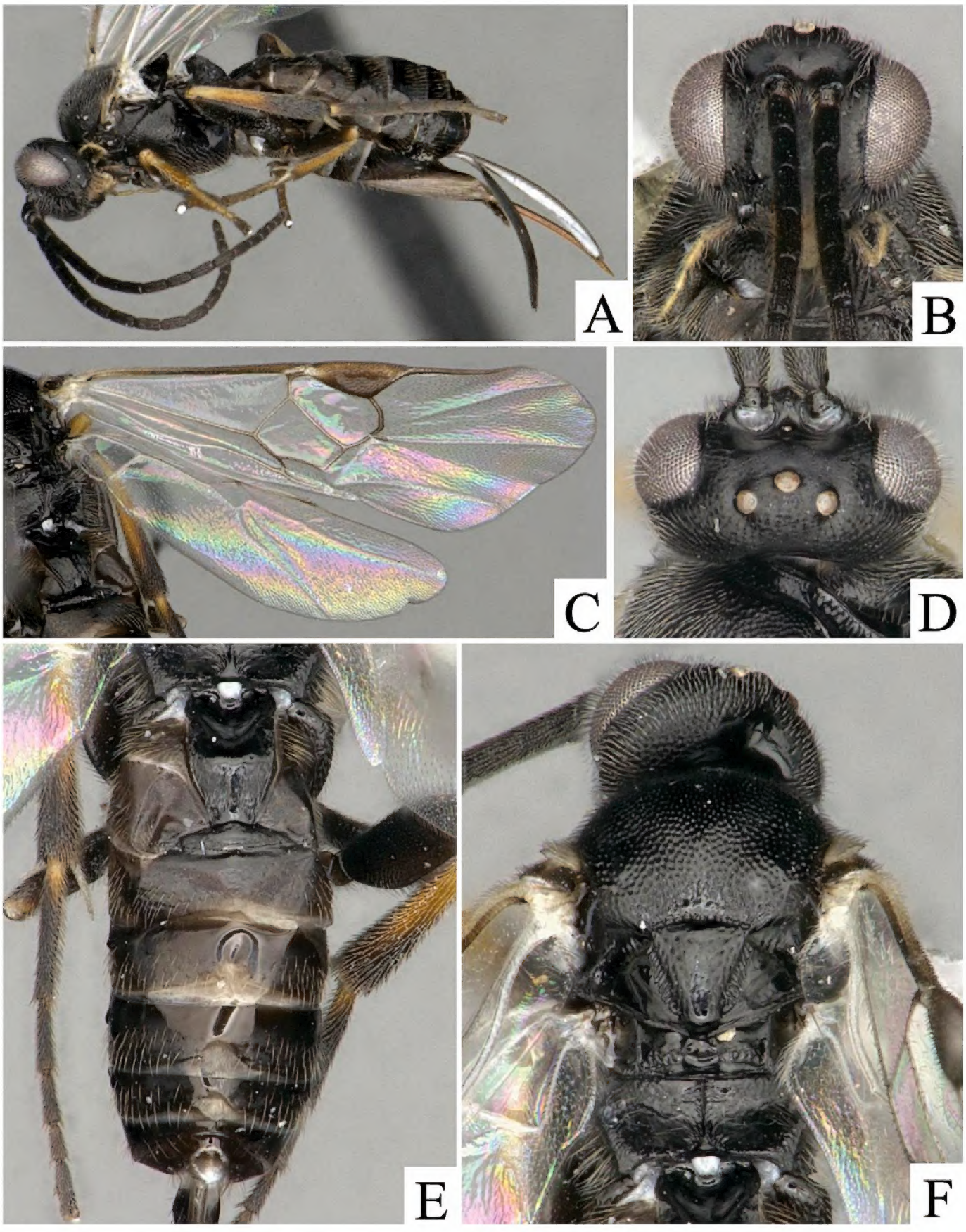

Figure 1. *Iconella melitaraevora*, female holotype **A** habitus **B** head, frontal **C** wings **D** head, dorsal **E** metasoma, dorsal **F** mesosoma, dorsal.

The most similar species is *I. etiellae*, which is the only other species so far recorded from New Mexico, among several other states in the central and western U.S.A. (Rodriguez et al. 2013; Fernandez-Triana et al. 2020). The main morphological differences between these two species are the hind leg color (metatibia entirely yellow and metatarsus almost entirely yellow in *etiellae*, metatibia with posterior half dark brown to black and almost entire metatarsus dark brown to black in *melitaraevora*); different size of ocelli

(ocular-ocellar line 1.6× posterior ocellus diameter in *etiellae*, 2.0× in *melitaraevora*); and T1 width slightly different (T1 width at anterior margin 2.4–2.5× T1 width at posterior margin in *etiellae* versus 2.0× in *melitaraevora*). Additionally, the longitudinal median carina on propodeum is more strongly defined in *etiellae* (much thinner and weak in *melitaraevora*), although this is a character difficult to assess unless several specimens from both species are at hand and available for comparison. The two species have different recorded caterpillar hosts within the Lepidoptera family Pyralidae (Table 1; *Etiella zinckenella*, *Melitara junctolineella*, *Psorosina hammondi*, and *Ufa rubedinella* for *etiellae*; *Melitara subumbrella* for *melitaraevora*). There are also molecular differences based on DNA barcodes (Fig. 2) with 43/552 bp different base pairs, or a 7.8% difference, between the two species *melitaraevora* (Process ID NACMA001-24) and *etiellae* (Process ID HYCNE1332-11). The combination of morphology, biology and molecular data allows us to separate and distinguish these two species. It is important to note that there are many undescribed species accessioned on BOLD, that are probably in *Iconella*, and the CO1 sequence data of this species differentiates it from those undescribed.

Body measurements and proportions (measurements of holotype provided first, followed, between parentheses, by range based on other specimens). Body L: 3.4 mm (3.2–3.5 mm). Fore wing L: 3.5 mm (3.5–3.6 mm). F2 L/W: 0.22 mm / 0.09 mm (0.22–0.23 mm / 0.10 mm). F14 L/W: 0.10 mm / 0.07 mm (0.10 mm / 0.07–0.06 mm). F15 L/W: 0.10 mm / 0.06 mm (0.10 mm / 0.06 mm). Metafemur L/W: 0.82 mm / 0.26 mm (0.82–0.83 mm / 0.26–0.27 mm). Metatibia L: 1.06 mm (1.02– 1.06 mm). Ovipositor L: 1.12 mm (1.14–1.18 mm). OOL: 0.14 mm (0.13–0.14 mm). POL: 0.15 mm (0.14–0.15 mm). OD: 0.07 mm (0.07 mm). T1 W anterior margin / W posterior margin: 0.32 mm / 0.12 mm (0.32 mm /0.12–0.13 mm). T2 W posterior

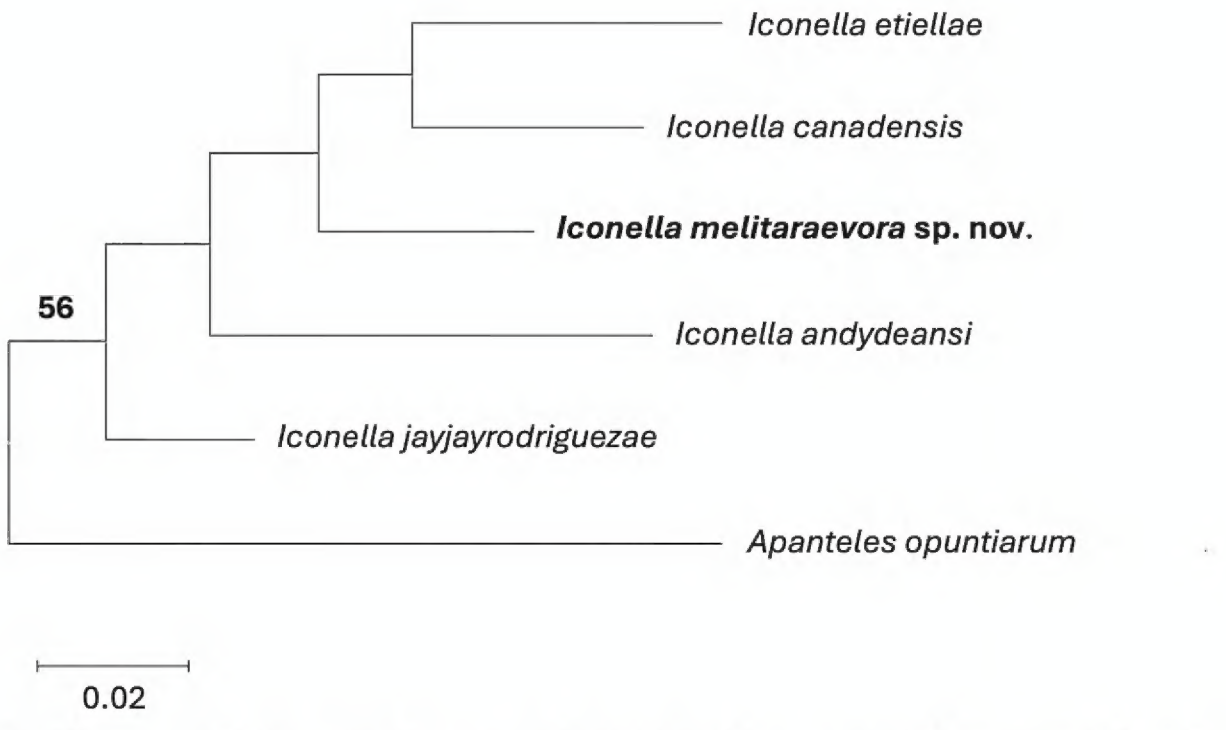

Figure 2. Maximum likelihood CO1 tree of described Nearctic and Neotropical *Iconella* species. *Apanteles opuntiarum* (Microgastrinae) from a laboratory culture originally collected in Santa Fe Province, Argentina was the outgroup. Bootstrap node support for the generic split is bolded. The scale bar is the nucleotide substitution rate visualized by the branch lengths.

margin /L: 0.44 mm / 0.11 mm (0.44–0.45 mm / 0.11–0.12 mm). Ovipositor sheath L / metatibia L: 1.06× (1.09–1.12×). Ocular-ocellar line / posterior ocellus diameter: 2.0×. T1 width at anterior margin/ T1 width at posterior margin: 2.4–2.6×.

Biology. The host for *I. melitaraevora* is *Melitara subumbrella*, a host-specific herbivore on *Opuntia* which has been recorded from three *Opuntia* species (Mann 1969). *Melitara subumbrella* larvae were collected on *O. phaeacantha* (Cactaceae, Fig. 3B), a mid to high elevation *Opuntia* distributed in dryland habitats of North America from Baja California, California, Nevada, Utah, Arizona, Colorado, New Mexico, Chihuahua, Oklahoma, and Texas. *Melitara subumbrella* larval feeding causes the host plant cladode tissue to swell and create a shelter, which resembles a "gall", and within which the larvae build tunnels and develop (Fig. 3B). This behavior and the associated plant-response is typical of shelter-building phycitine larvae that use *Opuntia* host plants (authors, unpublished data).

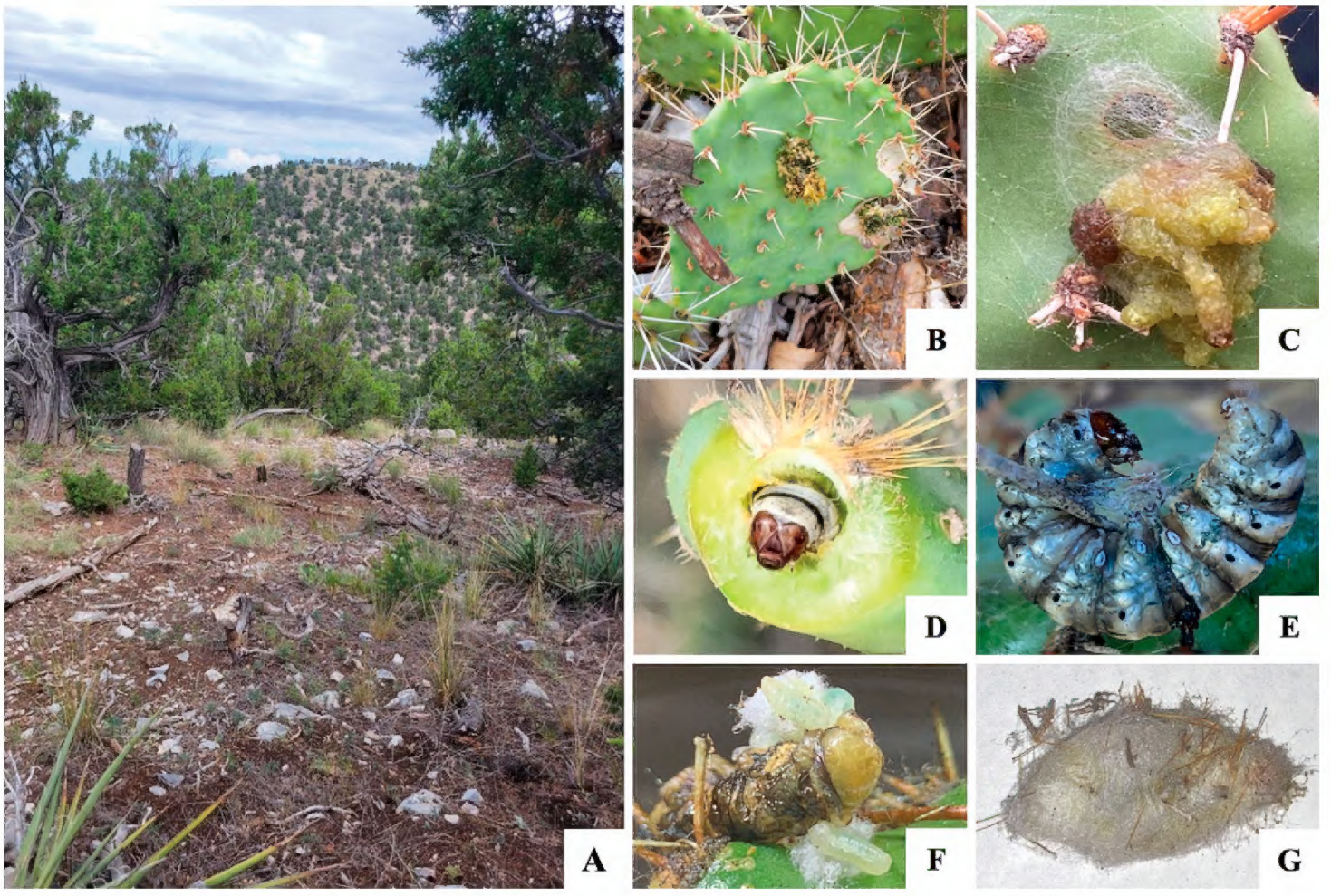

Figure 3. *Iconella melitaraevora* larval and host habitat images **A** Piñon-Juniper vegetation characteristic of the site where *I. melitaraevora* was collected in mid-elevation montane woodlands of Santa Fe County, New Mexico **B** host plant, *Opuntia phaeacantha* (Cactaceae) of *Melitara subumbrella* (Pyralidae) caterpillars, the wasp's larval host, exuded larval frass is visible outside the swollen shelter where the caterpillar develops **C** excavated hole that *M. subumbrella* larvae used to exude frass from the interior of the host plant, note that the hole is covered with silk to prevent intruders from entering **D** mature *M. subumbrella* larva inside a tunnel it has excavated within its host plant **E** parasitized, ultimate instar *M. subumbrella* larva, parasitoid larval emergence was imminent when this image was taken **F** gregarious *I. melitaraevora* larvae emerging from their host and spinning cocoons, see Suppl. material 1 for a video of this moment **G** silken puparium woven by *M. subumbrella* larva, within which *I. melitaraevora* larvae emerged from the host carcass to spin cocoons and pupate.

Twelve *M. subumbrella* larvae arrived at the laboratory alive. This number was based on the observation of conspicuous frass emission from host plant pads (Fig. 3B, C). Ultimate instar *Melitara subumbrella* larvae exited the host plant pads and formed puparia within the top 5 cm of soil. This behavior is also typical of *Opuntia* specialist phycitine larvae (Mann 1969). Five *M. subumbrella* larvae had *I. melitaraevora* larval cohorts emerge (Fig. 3F) and make cocoons within puparia that their caterpillar hosts constructed for pupation (Fig. 3G; Suppl. material 1). The wasp larvae were gregarious, with a range of 8–20 successfully emergent individuals per caterpillar cohort ($\bar{x}$ = 16 wasps ± 4 S.E.). Adult wasps from four of five cohorts emerged successfully, the reason for failed emergence of the final cohort is unknown. The sex ratio was female skewed with 28 females and 19 males reared, overall. However, one cohort had more males than females (9 ♀:10 ♂).

We do not know when *I. melitaraevora* oviposition took place in the field. But the *M. subumbrella* were clearly parasitized upon field collection on 23 August 2023 because they were held in containment for the duration of their development which precludes the possibility that they were attacked by other braconid wasps in transit from Santa Fe County, NM to Austin, TX. We observed larvae from one cohort emerge from the host and pupate on 10 December and another cohort was observed pupating on 18 December. Ultimately, two cohorts emerged on approximately 18 December 2023, the third emerged on 25 December 2023 and the fourth on 27 December 2024 (we did not observe the other two cohorts pupating). So, pupal development time was 7–8 days (N = 2), and total immature development was at least 15–19 weeks (N = 4) under laboratory conditions.

Updated key to *Iconella* from the New World

1 Metatibia mostly yellow, at most with very small and faint brown spot on posterior 0.1 or less; metatarsus mostly yellow, except for brown area on posterior half of first tarsomerus; fore wing with most veins transparent or white, vein margins of same color than interior of vein..... **2**

– Metatibia with brown to black coloration on posterior 0.2–0.5; metatarsus mostly dark brown to black, at most with yellowish area on anterior half of first tarsomerus; fore wing with at least some veins with thin brown margins and interior of veins yellow to light brown..... **3**

2(1) Pterostigma almost completely brown, with only small whitish spot anteriorly; humeral complex half yellow, half brown; profemur almost completely dark brown (yellow area absent or limited to posterior 0.2); distance between posterior ocelli 2.4× or more posterior ocellus diameter; T2 width at posterior margin 4.6× or less its central length; larger species, body length 3.0 mm or more and fore wing length 3.3 mm or more [Western and central United States (AR, AZ, CA, CO, IA, NM, OK, WA). Hosts: *Etiella zinckenella*, *Olycella junctolineella*, *Psorosina hammondi*, *Ufa rubedinella* (Pyralidae)] ..... ***Iconella etiellae*** **(Viereck, 1911)**

– Pterostigma mostly transparent or whitish, with only thin brown margins; humeral complex yellow to white; profemur mostly yellow, dark brown area limited to anterior 0.2 or less; distance between posterior ocelli 2.1× or less posterior ocellus diameter; T2 width at posterior margin 5.0× or more its length; smaller size, body length 3.0 mm or less, and fore wing length 3.2 mm or less [Caribbean islands and northern part of South America: British Virgin Islands, Cayman Islands, Dominica, Grenada, Guyana, Montserrat, Puerto Rico, Saint Kitts & Nevis, Trinidad & Tobago. Host: *Ancylostomia stercorea* (Pyralidae)] ..... ***Iconella isolata*** **(Muesebeck, 1955)**

3(1) Fore wing with pterostigma almost completely brown, with only small whitish spot anteriorly [USA: New Mexico. Host *Melitara subumbrella* (Pyralidae)] ..... ***Iconella melitaraevora*** **Fernandez-Triana, sp. nov.**

– Fore wing with pterostigma mostly transparent or whitish, at most with thin brown margins..... **4**

4(3) Ocular-ocellar line 1.6× posterior ocellus diameter; humeral complex half yellow, half brown; T1 1 width at anterior margin 2.2× or less T1 width at posterior margin; ovipositor sheaths length 0.8× or less metatibia length; larger species, body length 3.5 mm or more (rarely 3.2 mm), fore wing length 3.5 mm or more; an extra-tropical species distributed in North America north of 40°N (Canada) [Eastern Canada: NB, ON, and QC. Host: *Epinotia solandriana* (Tortricidae) and, likely, *Acrobasis betulella* (Pyralidae)] .... ***Iconella canadensis*** **Fernández-Triana, 2013**

– Ocular-ocellar line 2.0× or more posterior ocellus diameter; humeral complex fully yellow to white; T1 width at anterior margin 3.1× or more T1 width at posterior margin; ovipositor sheaths length 1.1× metatibial length; smaller size, body length 3.0 mm or less, fore wing length 3.3 mm or less; tropical species from Central America south of 17°N (Mexico and Costa Rica) **5**

5(4) Profemur mostly yellow, dark brown area limited to anterior 0.2 or less; meso- and meta- femora mostly dark brown, with proximal 0.1–0.2 yellow to orange; mesoscutellar disc sculpture centrally smooth with few, scattered punctures near margins; T2 width at posterior margin 4.1× or less T2 maximum length medially; body length 2.9–3.0 mm, fore wing length 3.2–3.3 mm [Costa Rica (Area de Conservación Guanacaste) and Mexico (Chiapas). Host: undescribed species of Phycitinae (Pyralidae) .... ***Iconella jayjayrodriguezae*** **Fernández-Triana, 2013**

– Profemur dark brown on anterior half, yellow on posterior half; meso- and meta-femora usually fully dark brown to black; mesoscutellar disc sculpture mostly with punctures scattered all over disc surface; T2 width at posterior margin 4.4× T2 maximum length medially; body length 2.7–2.8 mm, fore wing length 3.0 mm. [Costa Rica (Area de Conservación Guanacaste). Host: undescribed species of Spilomelinae (Crambidae)] .... ***Iconella andydeansi*** **Fernández-Triana, 2013**

Discussion

In November, temperatures fall below freezing daily, with permanent snow on the ground, in Santa Fe County, New Mexico. This extreme environmental condition provides some limitation on what the possibilities are for *I. melitaraevora* overwintering activity. One possibility is that *I. melitaraevora* overwinter as pupae within *M. subumbrella* puparia buried in the soil, until temperatures rise enough for the snow to thaw in the spring. Some portion of the wasps must be able to tolerate this cold period as pupae (Langer and Hance 2000), unless they can remain active as adults during the winter by attacking alternative hosts (Eoche-Bosy et al. 2016). In the spring, we predict that moths which survived winter diapause emerge, mate, and produce a new generation of larval hosts. In general, cactus moth flight activity does not commence until their *Opuntia* host plants begin growing new tissue that caterpillar larvae require for development (Morrison et al. 2025). The wasps documented here emerged in room temperature conditions in November and December 2023. Thus, the average immature development time that we measured may be considerably faster than what happens in the field. We predict that *I. melitaraevora* developmental phenology responds to favorable conditions, presumably those which facilitate host plant growth.

Until now, all *Iconella* species with known host information were solitary parasitoids (Whitfield et al. 1997). This is the first time that a gregarious *Iconella* species has been documented. The wasps in each cohort were probably oviposited by a single female, although it is possible they experienced super parasitism (Bakker et al. 1985; Varone et al. 2024), which is a rare phenomenon in the Micrograstrinae (Fernandez-Triana, personal observations). Regardless, all adults in each cohort emerged within 24 hours of each other which is within the fecundity range of gravid microgastrine females (Harvey et al. 2014).

All known American *Iconella* species attack shelter-forming lepidopteran larvae in the Pyralidae, Crambidae (Pyraloidea), and Tortricidae (superfamily Tortricoidea) (Whitfield et al. 1997; Fernandez-Triana et al. 2013). Most species in these superfamilies have shelter-building larvae (Lill et al. 2007), but these host superfamilies are not closely related within the lepidopteran clade Ditrysia (Regier et al. 2013). This suggests that *Iconella* are adapted to circumvent the behavioral manipulations that their hosts do to their food plants (Murdoch 1969; Ghimire and Phillips 2014). Host-finding mechanisms that *Iconella* species may use to locate suitable hosts include following volatile chemical compounds emitted by damaged host plants (Mbata et al. 2017; Turlings and Erb 2018), and homing in on caterpillar frass volatiles (Van Leerdam et al. 1985; Ngi-Song and Overholt 1997). A tight association with shelter-building larvae is also known from the braconid subfamily, Cheloninae. Chelonine females inspect leaf surfaces to find concealed host eggs into which they oviposit directly into developing larvae (Stireman III and Shaw 2022).

Iconella melitaraevora females may oviposit into hosts directly through *Opuntia* pads. The ovipositor is long enough (average *I. melitaraevora* ovipositor length = 1.12 mm) to penetrate an *Opuntia* epicuticle and reach the internal vascular tissue

where *Melitara* larvae feed (average *Opuntia* cuticle width = 0.05–0.10 mm thick, (Morrison et al. 2021). However, we think that this is unlikely because *Opuntia* pads are difficult for insects to penetrate with ovipositors (Jezorek 2011). The alternatives are that females enter pads through holes where *Melitara* larvae excrete frass (Fig. 3C) and attack larvae inside larval feeding cavities, or they attack when larvae expose themselves to excrete frass from the holes (Fig. 3D). In Argentina, *Apanteles opuntiarum* Martínez & Berta, 2012 (Microgastrinae) females attack *C. cactorum* larvae (Pyralidae, Phycitinae) after entering pads through the frass excretion holes as well as when larvae expose themselves outside pads to excrete frass (L. Varone, personal observations). Direct observation is required to confirm how *I. melitaraevora* oviposition takes place.

Iconella melitaraevora is now the second *Iconella* species documented to use cactus moth larvae as hosts in North America. The host, *M. subumbrella*, is distributed from Baja California to west Texas, north along the foothills of the Rocky Mountains to Colorado, and east into the plains of Oklahoma (Mann 1969). *Melitara* systematics is discordant with multiple phylogenetic hypotheses making species limits uncertain (Simonsen 2008; Regier et al. 2012; Roe 2014). So, the host distribution may be incorrect, or it could be that the *I. melitaraevora* host availability is considerable given this documented host distribution. *Iconella etiellae* has been reared from *Opuntia* specialist *Melitara junctolineella* caterpillars in Eastern New Mexico, as well as a variety of other shelter-building Pyralidae (Rodriguez et al. 2013; Fernandez-Triana et al. 2020). This indicates that *I. melitaraevora* may also attack multiple hosts. More shelter-building lepidopteran larvae from the area should be reared to determine if *I. melitaraevora* is host-specific to *Melitara subumbrella*, specific to *Melitara* species, or attacks a range of shelter-building lepidopteran larvae like its sympatric congener *I. etiellae.* There remains much to be learned of cactus moth trophic interactions, and of shelter-building Lepidoptera enemies in general given that likely only 10% of microgastrine species are described (Rodriguez et al. 2013; Fernandez-Triana et al. 2020).

Parasitism by coevolved Microgastrinae and other hymenopteran parasitoids accounted for 20% of invasive *Cactoblastis cactorum* (Lepidoptera, Pyralidae, Phycitinae) mortality in Argentina, its native range (Varone et al. 2019). Native range host testing with several South American Microgastrinae demonstrated that *A. opuntiarum* is specific to *C. cactorum* (Martínez et al. 2012; Varone et al. 2015; Folgarait et al. 2018). Follow-up sequential no-choice tests with North American cactus moth larvae, and phylogenetic relatives, confirmed that *A. opuntiarum* will be host-specific to *C. cactorum* in North America as well (Florida Dept. Agriculture & Consumer Services, unpublished data). Large-scale rearing capacity for *A. opuntiarum* has advanced significantly over the past decade (Awad et al. 2019; Srivastava et al. 2019; Varone et al. 2024) and the wasp was in the final stages of regulatory approval for release in the U.S.A. at the time of publication.

North American *Melitara* are parasitized by wasps in at least four families, including: Braconidae (Cheloninae and Microgastrinae), Scelionidae, Eulophidae,and Chalcididae (Mann 1969; Rodriguez et al. 2013; Morales-Gálvez et al. 2022; Villegas-Luján et al. 2024) and have patchy distributions (authors, personal observations), which

suggests that parasitoid pressure is high. Indeed, Mann (1969) also remarked how rare native cactus moth larvae were during a multi-decadal survey of *Opuntia* herbivores in the U.S.A. and Mexico. Given the shared biology and evolutionary proximity of American cactus moths, we hypothesize that some native North American cactus moth parasitoids in the Microgastrinae can utilize *C. cactorum* as a host and thus provide a level of natural biological control of this invasive species (Morrison et al. 2025). Ongoing studies and collections by groups at the Brackenridge Field Lab and Universidad Autónoma Agraria Antonio Narro (Saltillo, Mexico) are investigating this possibility.

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Supplementary material 1

Video of *Iconella melitaraevora* sp. nov. larvae emerging from its host, *Melitara subumbrella* (Lepidoptera: Pyralidae), to spin cocoons within which they pupated

Authors: Colin R. Morrison, Wyatt R. Armstrong, Robert M. Plowes, Lawrence E. Gilbert, José L. Fernández-Triana

Data type: zip

Explanation note: Available on GitHub via Zenodo at https://doi.org/10.5281/zenodo.14589691 (Morrison et al. 2024).

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Link: https://doi.org/10.3897/jhr.98.151036.suppl1